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Generalized Ecology and Life Cycles of Bark Beetles

R W. Stark

2. Generalized Ecology and Life Cycle of Bark Beetles

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Insects are a highly specialized group belonging to the large and diverse phylum of joint-legged animals, the Arthropods, which includes lobsters, crayfish, crabs, barnacles, shrimps, millipedes, centipedes, scorpions, spiders, mites and others. In terms of the number of species, it is the most successful phylum in the animal kingdom, and within Arthropoda, Insecta is the largest class. The evolutionary success of insects is, at least partly, attributable to several characteristics: flight, an external skeleton, metamorphosis, and specialized systems of reproduction.

The most obvious attribute of insects, shared only with birds and bats, is flight. Wings enable them to escape rapidly from unfavorable situations and to seek out favorable ones. Wings also enhance their ability to locate at a distance and forage widely for food. The external exoskeleton is composed of chitin, a substance that is flexible, lightweight, and tough, and is impervious to water, many chemicals, and most microorganisms. These characteristics have enabled insects to exploit habitats that soft-bodied forms would have to avoid. In addition, insects are able to regulate aspects of their reproduction in accordance with environmental cues. For example, some are capable of storing sperm and delaying fertilization until the proper food plants or conditions have been found, or delaying oviposition until the appropriate site is found or prepared.

The more primitive insects, such as grasshoppers, pass

through a gradual metamorphosis. The post-embryonic stages grow to adults with little change in appearance other than in body proportions, and the appearance of reproductive organs and wings. The immature stages of species that undergo gradual metamorphosis are known as nymphs and they exploit habitats similar or identical to those used by their parents. Complete metamorphosis consists of three distinct post-embryonic stages: an early form without wing pads called the larva, a quiescent form with wing pads called the pupa, and the adult. Members of the family Scolytidae, which contains bark beetles, undergo complete metamorphosis (Figure 2.1). In insects with complete metamorphosis, the egg may exploit one environment, the larva another, and the pupa and adult yet others. Further, metamorphosis can be accommodated to environmental conditions. Any one of the developmental stages may enter an arrested stage of development (diapause) that permits it to last out unfavorable periods. Some forms (e.g. multivoltine) have a facultative diapause, i.e., the onset is dependent upon environmental cues such as shorter day length. Others (e.g. immature stages of univoltine species) have an obligatory diapause, which is not influenced by environmental cues, i.e., it is genetically controlled. The most common obligatory diapause is winter diapause, which decreases mortality due to low temperatures, but summer diapause in response to drought or extremely high temperatures is not uncommon. In some species, developmental rate and time can be shortened or extended. For example, some species of bark beetles in the genus Dendroctonus are able to complete development at a rate that is primarily dependent on temperature and may complete from 4 to 7 generations in a single season.

The family Scolytidae (order Coleoptera) is one of the most successful in the class Insecta. Scolytids are subcortical feeding insects -- bark beetles and ambrosia or

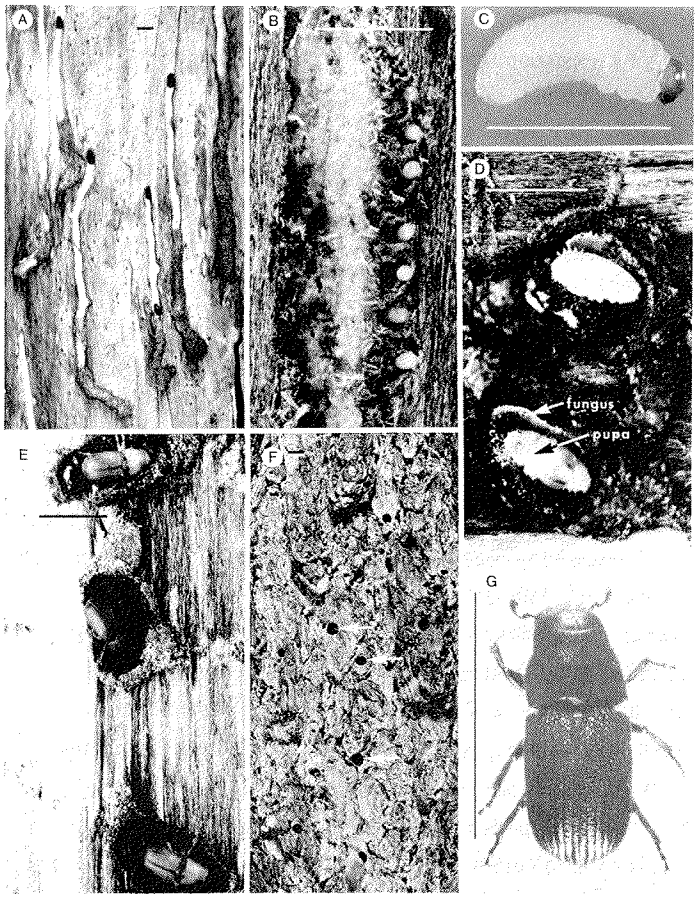

Figure 2.1. Stages in the life cycle of the western pine beetle, Dendroctonus brevicomis. (a) beetle galleries in phloem before eggs hatch. (b) eggs in niches in the parent gallery. (c) mature larvae. (d) pupal chamber with mature pupa surrounded by a mass of associated blue stain fungus. (e) newly formed adults beneath the bark. (f) exit holes left in bark. (g) mature adult.

timber beetles. They are distributed world-wide and there are many cosmopolitan genera. The bark beetles, in particular, have flourished in the coniferous forests of North America. The most destructive species are in the genus Dendroctonus (literally "killer of trees") whose hosts include all conifers and most hardwoods. There are about 24 known species of Dendroctonus in the world; 23 of these are found only in North America and one is found in Europe. Of the North American species, 19 are found north of Mexico, the remainder are in Mexico and Central America.

Scolytids occupy a broad range of niches on woody and herbaceous plants. Members of this family attack almost all forms of plant life, including coniferous and broad leaved trees, coffee, tea, sugar cane, cotton, rice, dates, corn, legumes, gourds, various fruits, cacti, and even corks of wine bottles. While ambrosia beetles are restricted to boles or large branches, bark beetles are not confined to any particular portions of plants and one or more species may be found attacking all plant parts. Primitive mouthparts, adapted for biting and chewing, have been retained in both the larval and adult stages and the well-developed mandibles enable them to penetrate and chew almost any material. They can tolerate a wide range of environmental conditions; some species can endure extremely high temperatures as well as those considerably below freezing. They can tolerate toxic substances such as conifer resin or resin vapor for long periods, and they can develop in oxygen-deficient environments. Some can withstand long periods without water. Scolytids possess highly sophisticated systems of communication based primarily on chemistry (Chap. 4) and sound and they have developed symbiotic (Chap. 6) and communal relationships (Chap. 5, 10) with several types of

organisms. Each of these features has contributed to the evolutionary success of these organisms.

The literature on the family, particularly on those species of economic importance, is extensive but there are several good general references (e.g. Anderson 1960, Baker 1972, Bright and Stark 1973, Chamberlin 1939, 1958, Graham and Knight 1965, Graham 1963, Furniss and Carolin 1977, Rudinsky 1962, Thatcher 1960, Wilson 1977). The family contains about 73 genera and over 625 species with a potential for injury to plant life that is awesome. Fortunately, however, relatively few have been elevated to

Table 2.1. Important Forest Scolytidae of North America north of Mexico[1]

Dendroctonus adjunctus	Roundheaded pine beetle
D. frontalis	Southern pine beetle
D. brevicomis	Western pine beetle
D. engelmanni (= *D. obesus*)	Engelmann spruce beetle
D. jeffreyi	Jeffrey pine beetle
D. ponderosae	Mountain pine beetle
D. pseudotsugae	Douglas-fir beetle
D. valens	Red turpentine beetle
Hylurgopinus rufipes	Native elm bark beetle
Ips plastographus (= *I. integer*]	California pine engraver
I. lecontei	Arizona five spined engraver
I. pini (= *I. oregonis*)	Pine engraver
Scolytus multistriatus	Smaller European elm beetle
Trypodendron lineatum	Striped ambrosia beetle

[1]From Davidson and Prentice 1967.

the status of pests of national importance (Table 2.1). Eight species of Dendroctonus and only the ambrosia beetle, Trypodendron lineatum, are considered serious pests and this list has remained remarkably constant for many years. For example, for as long as we have records from the Pacific Northwest, the fir engraver beetle, Scolytus ventralis, has been a significant pest in the true fir forests and in the Southeastern U.S., the black turpentine beetle, Dendroctonus terebrans, continues to cause extensive damage to pines, particularly in turpentine orchards (Baker 1972).

GENERALIZED LIFE CYCLE OF SCOLYTIDS

The extreme variety of life cycles in the family Scolytidae mandates some restrictions in coverage. The ambrosia or wood-boring species deserve some mention but this chapter will emphasize the tree killing bark beetles (Dendroctonus) whose life cycle is passed largely in galleries completely or partially excavated in the phloem of conifers.

Ambrosia Beetles

The ambrosia beetles are wood-boring species that utilize either the bole or branches of their hosts, and almost all species in North America infest only dead or dying trees. Their name is derived from their symbiotic relationship with ambrosial (describing the food of Greek and Roman gods) fungi which the beetles introduce into breeding galleries and tend and harvest for food. Adults of some species actually

collect the fungal spores and place them near the developing larvae. Both sexes participate in maintaining the galleries clear of boring dust and frass, although it has been claimed that some adult and larval excrement is retained to "fertilize" the fungal gardens.

There are both monogamous and polygamous species. Either the male or female selects the host, excavates an entrance tunnel, and is joined by its mate. They excavate egg galleries deep in the xylem (Figure 2.3), where they establish their fungus "gardens" and where the larvae develop. Eggs may be deposited more or less indiscriminately along the gallery walls or in individual cradles or burrows. The larvae feed on the ambrosial fungi and, as adults, they emerge from the parental entrance hole or bore directly out through the wood and bark.

Bark Beetles

For convenience the life cycle will be treated in three phases (Figure 2.2); Dispersal, which includes emergence from the host tree, flight to a new host tree, and selection of that host for establishment of the next generation; Colonization, the process of invading the tree and initiating the brood gallery; and production, which includes mating, egg gallery construction, egg deposition or oviposition, and brood development up to the time of emergence (Cobb et al 1968; Wood 1972).

Dispersal. Once the adult bark beetle has fully developed (Figures 3.1-3.5) it constructs an exit hole from the pupal cell by boring directly through the outer bark, leaving

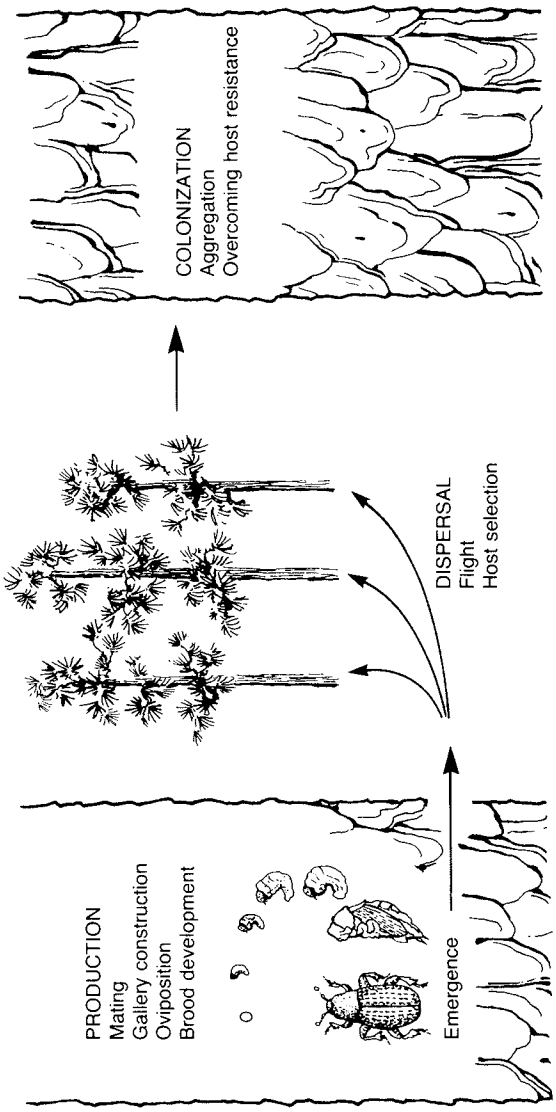

Figure 2.2. Life cycle of a representative bark beetle. The cycle may be broken into 3 stages: production, dispersal, and colonization.

a distinctive clean cut hole in the bark. The bark of abandoned trees is literally riddled with these holes. Emergence takes place over a period of several days or weeks. The sex that emerges first is usually the species that selects the host tree; these are generally females in the genus Dendroctonus. Environmental conditions, particularly temperature, significantly affect emergence and dispersal. For example, there is a typical temperature threshold below which beetles cannot fly, and an upper temperature limit that inhibits flight, and both emergence and development vary with altitude and latitude, probably also as a function of temperature.

There are many factors which influence the direction and duration of flight. In the Trypodendron species, for example, emerging beetles have a "gas bubble" in their gut that must be eliminated by flight exercise before the insect will settle on a substrate, thereby insuring dispersal (Graham 1959). Although bark beetles are capable of long distance flight, they generally attack trees in the vicinity of the brood tree from which they emerged.

There is a considerable mystery surrounding the ability of beetles to locate and select hosts. Some investigators believe that a "primary attraction" exists that results from odors emanating from physiographically weakened trees (Person 1931, Heikkenen 1977). Others believe that dispersing beetles land randomly on host and non-host trees (Chap. 9), perhaps guided initially by visual cues (Gara et al. 1965). Whether the beetles continue to the next phase, colonization, depends on their acceptance of the tree as an appropriate host (Borden 1974). The "host selection principle" asserts

that insect species will attack the host species in which they developed as larvae (Walsh 1864, Craighead 1921). Others have shown that photic reactions are important in flight, dispersal, and orientation to the host (Rudinsky 1962, Schonherr 1976, Shepherd 1966), for some bark beetles respond to profiles of the tree crown, others to vertical (living tree) and horizontal (fallen tree) shapes. Initial attraction and host selection are still open questions and are, consequently, areas of active research.

Host preferences shown by scolytids are presented in Appendix 1 (Baker 1972, Chamberlin 1958, Bright and Stark 1973). Care must be taken when drawing conclusions from such host lists because they reflect the intensity and accuracy of collection records, and are subject to the idiosyncracies of taxonomists.

Colonization. The acceptance of a suitable host tree by a pioneer beetle begins the colonization process. Feeding in the host has been divided into three categories: (1) monophagy-feeding on host plants of one or more closely related species within a genus; (2) oligophagy-feeding on species in several genera within a family and (3) polyphagy-feeding on species in several families. There are many different classifications of coniferous trees that express various authors' opinions of their evolutionary or taxonomic relationships. This presentation relies upon the review of Harlow and Harrar (1941). Generally, it may be stated that a higher degree of monophagy is demonstrated by those species that attack living trees (e.g. Dendroctonus, Ips) whereas species with polyphagous habits are those attacking primarily dead or downed trees (e.g., the ambrosia

beetles, Trypodendron, Gnathotricus) (Table 2.2 and Appendix 1). With few exceptions, (e.g. certain Micracisella, Xyleborus), species attacking conifers do not attack hardwoods. For example, the genus Micracisella is restricted mainly to hardwoods and six of the eight species

Table 2.2. Feeding Habits of Scolytidae[1]

Genus	No. spp. Considered	Monophagous[2] M-1	Monophagous[2] M-2	Oligophagous	Polyphagous
Scolytus	11	0	3	8	0
Crypturgus	4	0	0	3	1
Dolurgus	1	0	0	1	0
Polygraphus	2	1	0	1	0
Carphoborus	5	1	0	4	0
Phloeotribus	2	1	0	1	0
Dendroctonus	12	4	4	4	0
Phloeosinus	23	12	2	7	2
Xylechinus	2	0	0	1	1
Scierus	2	0	0	2	0
Pseudo-phylesinus	11	2	2	6	1
Hylastes	8	1	2	5	0
Hylurgops	5	0	3	2	0
*Trypodendron	4	0	0	2	2
Cryphalus	5	1	1	2	1
*Gnathotricus	4	0	0	1	3
Conophthorus	10	8	2	0	0

Table 2.2 (continued)

Genus	No. spp. Considered	Monophagous[2] M-1	Monophagous[2] M-2	Oligophagous	Polyphagous
Pity-ophthorus	52	15	25	12	1
Ips	22	6	12	4	0
Micracis	1	0	0	0	1
Pityogenes	7	1	3	3	0
Pityokteines	5	0	1	4	0
Orthotomicus	1	0	0	1	0
Pityokteines	1	0	0	1	0
*Xyleborus	9	0	1	0	7
Dryocoetes	6	1	3	2	0

*ambrosia beetles

[1]summarized from Appendix 1

[2]M-1, feeding on a single species in a genus
M-2, feeding on several species in a genus

of ambrosia beetles in the genus Xyleborus (listed in Appendix 1) feed primarily in hardwoods; the remaining two are confined to conifers.

There is a continuing controversy over whether scolytids are "primary" or "secondary" insects, i.e. whether they are able to overcome completely healthy trees in full vigor or only those trees of subnormal physiological condition (Rudinsky 1962, Amman 1978, Shrimpton 1978). Under endemic conditions the preponderance of species are termed "secondary", that is, they infest living trees of subnormal

physiological condition, which have been temporarily or permanently weakened by drought, defoliation or disease, or have been fatally injured by cutting, fire, or windthrow. These authors agree that it is under epidemic or outbreak conditions that many species become primary pests and invade and kill trees in apparently normal health. The major areas of controversy center on whether epidemics are caused when large tracts of trees become weakened and susceptible to attack or when beetle populations experience genetically controlled behavioral changes causing them to become more aggressive and overcome normally resistant trees (see also Chap. 9).

Whatever the stimuli, successfully attacking beetles initiate a complex chain of events leading to colonization of the tree. Once a few beetles have successfully entered the bark of the selected host, aggregation of individuals of both sexes commences. This is a critical phase of the bark beetle life cycle, for the defenses of a living tree, even stressed trees, are formidable. Most conifers contain copious quantities of oleoresin with toxic properties and so a large number of beetles are needed to successfully attack a healthy tree (see Chap. 3, 9).

Aggregation on the host tree is regulated almost exclusively by pheromones, which are produced by the attacking beetles, in conjunction with host volatiles that synergize or activate the pheromones. This "secondary attraction" involving pheromones has been found in over 60 species of scolytids from some 20 genera (Borden et al. 1975). Because of their importance to the understanding of bark beetle life histories and in management, pheromones are discussed at length in Chapter 4.

The organs which detect pheromones (sensilla) are located on the antennae. There are literally hundreds of sensilla with thousands of receptor pores. Airborne molecules of the pheromones and host odors are collected and transmitted through the central nervous system, and elicit behavioral responses. The pheromones are released by one species to attract members of that same species but they also attract parasites, predators, and commensals of bark beetles (Chap. 5).

Spacing of gallery sites on the host tree and the density of attacks by bark beetles are controlled by a weakening or cessation of the attractant pheromone, by release of repellent pheromones, or by stridulation, which is the production of sound by friction. Stridulation is highly developed in scolytids. Barr (1969) reviewed the world literature and found that 77 species in 23 genera were known to possess stridulatory mechanisms. Possession of a stridulatory organ appears to be associated with the sex opposite to that which initiates the entrance tunnel. Apparently specific "signals" are associated with different kinds and timing of stridulations. Stridulation has been associated with stress, rivalry and aggression, "greeting", or with courtship in D. valens, D. ponderosae, D. pseudotsugae and D. frontalis (Rudinsky and Michael 1974, Ryker and Rudinsky 1976, Rudinsky and Ryker 1976). In D. ponderosae and D. brevicomis, male stridulation elicits release of pheromone by the female (Rudinsky et al. 1976).

Removal of stridulating organs of Ips confusus females resulted in their entrance to the gallery being denied or delayed by the males, although once they were admitted, there was no significant difference in egg gallery construction.

The state of our knowledge and understanding of sonic communication is embryonic and offers another area where much more research is warranted.

Microorganisms, such as the blue stain fungi of the genus Ceratocystis (Chap. 6), play important roles in the colonization phase (Francke-Grosmann 1963, Graham 1967, Safranyik et al. 1975, Shrimpton 1978). They probably influence aggregation, modify development and survival by providing nutrients and assist in overcoming the natural defense mechanisms of the tree (Chap. 7). For example, fungi, which are transported by the southern pine beetle in special structures called mycangia, influence the production of pheromones by the beetle (Brand et al. 1976, Brand and Barras 1977).

Production. Successful entry to the phloem in the bark-wood interface signals the beginning of the production phase of the life cycle. After attacking bark beetles have penetrated to the phloem layer, they begin construction of the brood gallery. Many species, particularly the polygamous ones, excavate a nuptial chamber for mating. Individual egg galleries for each female radiate from this chamber (Figure 2.3). The nuptial chamber is usually kept free of boring material and frass and may be visited from time to time by the females. By contrast, monogamous species generally mate on the bark surface near the entrance hole or in the tunnel in a "turning" niche. Although most monogamous species mate but once, some (e.g. most Dendroctonus species) can re-emerge and initiate a second gallery in the same or another host tree. It is not known whether re-emerging beetles will mate again but this phenomenon has important implications for population dynamics (Chap. 8).

Bark beetle tunnels or galleries are of many types and often so characteristic of a species that they serve for species identification (Figure 2.3d-g). The principal gallery is excavated for the deposition of eggs but many species also excavate ventilation and food tunnels. Ventilation tunnels are bored by the adult from the egg gallery through the bark to the outside. They are most common in species which have long egg galleries. It is assumed that the principal purpose is for ventilation but they serve other purposes such as outlets for frass and boring dust. They are also utilized by parasites and predators to gain entry into the bark beetle gallery. Food tunnels are usually extensions of the main egg gallery or of the pupal chambers that are excavated by those species which mature in the fall but which overwinter under the bark and do not emerge until the following spring. Some species feed in portions of the host other than where they establish their egg galleries, i.e. in buds, small twigs or outer bark.

The egg gallery of all bark beetles is almost invariably in the phloem; the larval galleries and pupal cells of most are also in the phloem but in Dendroctonus brevicomus, the western pine beetle, third and fourth instar larval mines and pupal cells are excavated in the outer bark. Some species keep the egg gallery free of frass and borings while others pack this material behind them as they excavate. This chore is usually done by the male, and in polygamous species with up to 8 or 10 females the task becomes comparable to that of Hercules in the Stygean stables! It has been suggested that clean galleries facilitate repeated copulation in polygamous forms. Special morphological adaptations have evolved to accomplish frass removal. For example, the elytral declivity

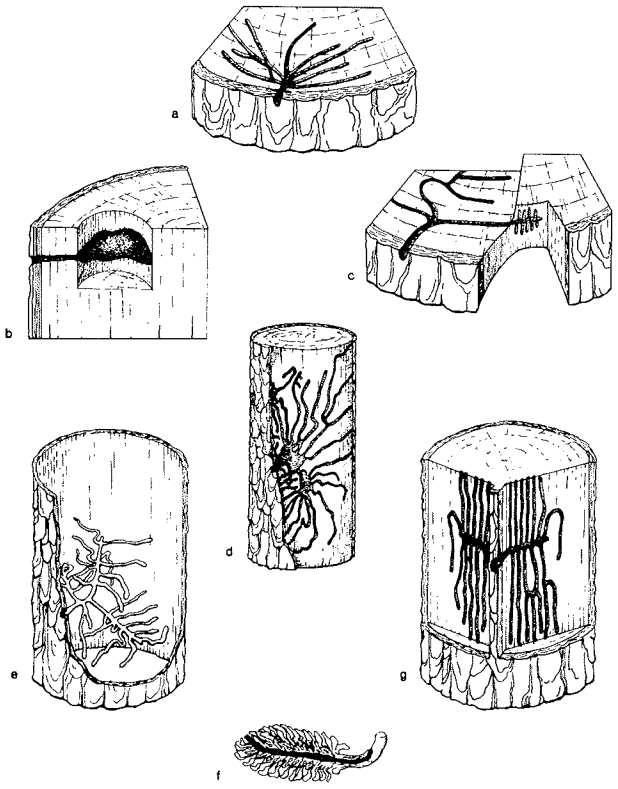

Figure 2.3. Ambrosia (a-c) and bark (d-g) beetle galleries. (a) branched type e.g. Xyleborus spp. (b) cave type e.g. Xyleborus spp. (c) compound type e.g. Trypendron, Gnathortricuss spp. (d) cave type, Renocis heterodoxus. (e) radiate or star-shaped, Pityokteines elegans and Taenioglyptes, Ips spp. (f) cone beetle type Conophthorus spp. (g) forked tunnels, Leperisinus californicus and Scolytus, Alniphagus, Pseudohylesinus spp. Redrawn from Chamberlin (1958).

in Ips and Scolytus at the posterior is modified somewhat like a specialized bulldozer or shovel (Figure 3.4). Other modifications include rake-like tibiae, flattened or concave head capsules, and dense hairiness (a mobile broom!).

The number of eggs laid by bark beetles varies widely from as few as 6-8 in Hylastinus obscurus to as high as 300 in Dendroctonus ponderosae. The more destructive species are the more fecund. Eggs are laid in various patterns, along each side of the egg gallery (Figure 3.4). These may be spaced regularly, close together or distinctly separated, and they may be opposite one another, or alternated. A single egg is placed in each niche and covered with frass. Egg grooves are made by the Douglas-fir and Engelmann spruce beetles in which 20 or more eggs are placed. In cave type galleries, eggs may be deposited loosely without any apparent order, in niches or at the end of short tunnels, in small clumps around the margin, or in masses encompassing all parts of the margin (Figure 2.3d). The period during which egg deposition occurs varies considerably among species but invariably is restricted to spring, summer or early autumn. Only a few species over-winter in the egg stage and then only in warmer climes.

Larval mines may be bored in the same plane as the egg, e.g. entirely in the phloem (Figure 2.3), extending directly to the outer bark or sapwood, or show a combination of both characteristics. The mines increase in size as larvae grow, and are usually packed with frass and borings. Typical mines vary in length from a few mm to up to 5 cms. When the larva has reached maturity it excavates a slightly larger cavity, a pupal cell, in which it transforms to the pupal stage (Figure 2.1).

Newly transformed adults of bark beetles pass through a stage as callow or teneral adults during which the exoskeleton hardens and sexual maturation is reached (Figure 2.1). Soon after they mature, they excavate an exit hole from their pupal cell to the outside. Some species feed for a few days or even weeks before exiting. Species maturing in the fall may pass the winter as young adults, emerging when external temperatures are suitable. The adult of other species however, may leave the host tree and over-winter in the duff and litter of the forest floor, in deep cracks or crevices of the bark, or may even excavate hibernation tunnels in the bark near ground level. Various cone-inhabiting species may hibernate one or more winters in cones on the forest floor, or on lichen-covered limbs. One bark beetle species constructs special hibernating tunnels in which 12-20 other species may be found!

As might be expected from the latitudinal and altitudinal distribution of bark beetles, a great diversity in seasonal development occurs. This variation occurs within species as well as between. For example, in Canada the western pine beetle has only one or one and a partial second generation per year. In its most southerly location in California, three and a partial fourth generations may develop (Miller and Keen 1960). The mountain pine beetle (D. ponderosae) normally has one generation per year, but at higher altitudes and latitudes may require two years to complete a generation (Amman 1973). For the southern pine beetle, the number of generations per year may range from 2-3 in the northern part of its range to 7 or 8 in southeastern Texas, depending on the warmth and length of the season (Thatcher 1960, Coulson et al. 1979a). Hibernating adults usually emerge first,

followed by those that passed the winter as newly formed adults, then those that passed the winter as pupae, then those that passed the winter as larvae. Only a few generalizations can be made about the timing of emergence. One is that scolytids are remarkably adapted to prevailing weather and climate and can adjust their emergence accordingly, although all species seem to have "peak" periods of emergence and attack. Another is that, in colder portions of their range, few, if any, over-winter in the two most vulnerable stages, eggs and pupae. The cone beetles (Conophthorus spp.) and perhaps others, exhibit an unusual survival mechanism in that not all individuals of a brood emerge the first year. This is probably an adaptation to cope with the normal periodicity of cone crops. Cone beetles may also, on occasion, become twig borers or they may feed on the bark and phloem at the juncture of two small twigs.

SCOLYTIDS IN FOREST ECOSYSTEMS

Since ecology is a relatively young science, few fundamental principles go unchallenged. Ecology is really a debate. This complex subject must be approached with some temerity, particularly since the ecological role of insects in forest ecosystems has been poorly studied. Further, scolytids are but one small component of the abundant and diversified insect fauna inhabiting forests. Although we are concerned here only with conifers, many broad-leaved trees, plants and shrubs also serve as hosts for bark beetles. Thus, the total

influence of scolytids on forests cannot be fully described in this restricted treatment. We can, however, suggest some probable significant influences of tree-killing scolytids on three fundamental ecological processes: natural selection, primary production, and forest succession.

Natural Selection

A forest ecosystem consists of a community of organisms plus its physical environment. The community, in turn, consists of populations of several species whose activities are interdependent. The genetic structures of the populations strongly influence the ways in which the populations interact, and the levels of genetic diversity that we see in the populations are, in turn, strongly influenced by spatial and temporal variation in the environment. Changes in the environment affect different genotypes differently and the differential reproduction of genotypes is what we call natural selection.

The tree-killing Scolytids, e.g. most Dendroctonus, act as one of the forces of natural selection exerting substantial pressures on their host trees. Of course, so too have the trees exerted selective pressures on the beetles (Chap. 10). Over the long history of their coexistence, the beetles have eliminated highly susceptible trees from the forest. By their preference for physiologically weakened trees, bark beetles help to keep the forest free of diseases. But other forces continue to generate trees which vary in their ability to resist attack. Older trees are less resistant, as are trees that have been weakened by stresses such as disease,

fire, or smog. Other trees vary in their ability to produce large quantities or different types of toxins. As long as there is a genetic component to the differences in susceptibility among the trees, bark beetles will continue to influence the evolution of their hosts.

Primary Production

Primary production is viewed as a product of the amount of photosynthetic biomass present in the system and the average rate of net photosynthesis. Scolytids influence primary production directly by reducing biomass and net photosynthesis by killing whole trees (e.g. Dendroctonus), or by killing the tops of trees (e.g. by Ips and Pityophthorus). However, often these trees are already weakened or senescent; their photosynthesis is not in excess of their respiration, so they are not growing. Tremendous quantities of organic molecules (and energy) are stored in these trees and, by killing them, scolytids accelerate the recycling of these nutrients. Elimination of these trees allows growth to occur in the more vigorous trees in the stand. Therefore, cropping by beetles may actually increase primary production in the forest. In comparison with vertebrate and other invertebrate herbivores, insects consume proportionately more energy and, therefore, they make more energy available to other consumers in the ecosystem (Price 1975). Mattson and Addy conclude that

> Insect grazers function much like cybernetic regulators of primary production in natural ecosystems. That is, they tend to ensure consistent and optimal

> output of plant production over the long term for a particular site. Their actions or activities seem to vary inversely with the vigor and productivity of the system. This inverse relation is probably a consequence of the long history of coevolution between plant systems and their usual consumers.
>
> (Mattson and Addy 1975)

Forest Succession

Plant species may occupy a particular area if the physical and biotic factors meet the requirements of the plant. If the environment stayed constant the species could theoretically remain there forever. Environmental conditions do change, however, and many of the changes are induced by the species naturally inhabiting the site. As conditions change so do the plants occupying any particular site. For example, the first species of tree established at a site may be replaced by more shade-tolerant species. The process of change in plant communities over time is called succession. Scolytids, particularly the tree-killing Dendroctonus species, play an integral role in natural forest succession. For example, extensive outbreaks of the spruce beetle D. rufipennis Kby. in Alaska (Baker and Kemperman 1974) and Colorado (Schmid and Hinds 1974, Schmid and Frye 1977) killed most of the spruce, which dominated the stands, and returned the forests to earlier stages of succession dominated by shade intolerant species.

The effects of scolytids on forest succession is best explained by examining a single example in some detail.

Lodgepole pine ecosystems and the role of mountain pine beetle in them have been studied extensively (Amman, 1977, Pfister and Daubenmire 1975, Roe and Amman 1970, Wellner 1978). Lodgepole pine (LP) plays four basic successional roles in various plant series (see Chapter 9 for management implications). These are:

Minor seral. LP is a minor component of young even-aged mixed stands. Due to its rapid growth habit it assumes dominance early in succession but it does not regenerate well. It is gradually eliminated from the forest as mortality increases from age 50-200 years. The mountain pine beetle hastens this process by attacking the larger (60-80 year old) LP.

Dominant seral. LP is the dominant cover type of even-aged stands with a vigorous understory of shade-tolerant species that will normally replace LP in 100-200 years. The beetle could hasten this process as above, but, because LP is the dominant cover type, extensive outbreaks lead to a build-up of dead trees that constitutes an extreme fire hazard. The beetle kill, followed by an intense wild fire, returns the forest to the earliest stage of succession where LP once again dominates.

Persistent. Even-aged stands of LP are the dominant cover type and there is little evidence of replacement by other species. Again the beetle and fire have acted in concert over long periods to favor LP. Elimination of LP by the mountain pine beetle returns the forest to an earlier stage of succession, e.g. brushfields, which will be taken over by LP once again.

Climax. LP is self-regenerating. Such climax forests of LP are infrequent, occurring only in habitats unsuitable for other conifers. In these, destruction of the LP results in conversion of the habitat to other plant species.

Lodgepole pine and the mountain pine beetle have probably coexisted since the trees' earliest existence (Amman 1977, Roe and Amman 1970) so the potential for their coevolution has been great. Peterman (1978) suggested that mountain pine beetles may decrease the probability that stands of LP with predominately serotinous cones would stagnate. The age at which LP becomes susceptible to the mountain pine beetle (70-80 years) coincides with maximum cone production. Continued cone production long after this time results ultimately in so much germination that competition among seedlings reduces survival. Thus, beetle kill at age 70-80, followed by fire, releases the seeds from the serotinous cones at a time that ensures maximum survival of the lodgepole pines and therefore of the food supply of the beetle.

This brief overview of the major roles of scolytids in forest ecosystems does not do justice to the multitude of intricate relationships of the many scolytids present in forests. Nor can one point to a single reference, or even several, where such information is available. Long term ecological research necessary to elucidate involvement of scolytids in ecological processes is generally lacking. There is little question, however, that tree-killing scolytids and their coniferous hosts have co-evolved.

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